A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

NeoBiota 98: 43–59 (2025)
DOI: 10.3897/neobiota.98.139097

Research Article

Milkweed (*Asclepias syriaca*) invasion, forest-steppe fragment size and isolation jointly constrain arthropod communities and their functional traits

Róbert Gallé[1,2,3], Ágota Réka Szabó[1,4], Edina Török[1], Tamás Lakatos[1,4], Dávid Korányi[1], Attila Torma[1,5], Nikolett Gallé-Szpisjak[1], Péter Batáry[1,2]

1 *'Lendület' Landscape and Conservation Ecology, Institute of Ecology and Botany, HUN-REN Centre for Ecological Research, Alkotmány út 2-4, 2163 Vácrátót, Hungary*
2 *National Laboratory for Healty Security, HUN-REN Centre for Ecological Research, Alkotmány út 2-4, 2163 Vácrátót, Hungary*
3 *MTA-SZTE 'Momentum' Applied Ecology Research Group, Közép fasor 52, 6726 Szeged, Hungary*
4 *Doctoral School of Biology, Institute of Biology, Eötvös Loránd University, Pázmány Péter sétány 1/C, 1117 Budapest, Hungary*
5 *Department of Ecology, University of Szeged, Közép fasor 52, 6726 Szeged, Hungary*
Corresponding author: Róbert Gallé (galle.robert@ecolres.hu)

Abstract

Habitat fragmentation has far-reaching negative impacts on the environment, resulting in biodiversity loss, soil quality degradation and alteration of water availability. In addition, fragmentation can disrupt ecological processes, potentially facilitating the establishment and spread of invasive plants, which can further harm native arthropod communities and alter their ecosystem dynamics. However, the exact nature of these impacts may vary depending on local conditions. We investigated the impact of fragmentation and milkweed invasion on invertebrate communities in sandy grasslands of forest-steppe habitats in Hungary. We selected 30 grasslands in forest-steppe fragments, varying in size (0.2 to 8.7 ha) and connectivity (Hanski's connectivity index: 0 to 705). We sampled ground-dwelling arthropods, mainly herbivores (true bugs) and predators (spiders), with pitfall traps and pollinators (wild bees) by direct observations along transects in invaded vs. non-invaded patches (min. of 500 m^2) of each fragment. We considered arthropod species' body size (all groups), dispersal ability and feeding (herbivores and predators) and nesting location and social habit (wild bee) traits in our analyses. In non-invaded patches, the number of monophagous herbivores showed an increasing trend, whereas in invaded fragments, there were more polyphagous individuals with increasing connectivity and fragment size. The dispersal ability of predators was lower as connectivity increased in non-invaded patches but higher in patches invaded by milkweed. We found more ground nesting bees in the invaded patches of small fragments than in large fragments, however, we did not find a significant effect in non-invaded patches. In summary, we often found interacting effects of the studied variables, fragmentation and invasions, generally modifying each other's effect by filtering for opposite trait levels. The primary objective of restoration projects should be restoring habitat of appropriate size and connectivity and eradicating invasive species while concurrently supporting the revival of native species and their ecological relationships. It is essential to employ adaptive management techniques, including continuous monitoring, to effectively tackle the interaction between fragmentation, invasion, and the preservation of biodiversity.

Key words: Biodiversity loss, connectivity, functional diversity, habitat degradation, landscape structure, sandy grassland

OPEN ACCESS

Academic editor: Deepa Pureswaran
Received: 15 October 2024
Accepted: 10 January 2025
Published: 21 March 2025

Citation: Gallé R, Szabó ÁR, Török E, Lakatos T, Korányi D, Torma A, Gallé-Szpisjak N, Batáry P (2025) Milkweed (*Asclepias syriaca*) invasion, forest-steppe fragment size and isolation jointly constrain arthropod communities and their functional traits. NeoBiota 98: 43–59. https://doi.org/10.3897/neobiota.98.139097

Copyright: © Róbert Gallé et al.
This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International – CC BY 4.0).

Introduction

Land-use changes, such as afforestation of grasslands, urbanisation and agricultural expansion, result in the fragmentation of natural habitats (Fischer and Lindenmayer 2007). Habitat fragmentation *per se* is independent of habitat loss, for a given amount of habitat, a more fragmented landscape has more, but smaller habitat patches (Fahrig 2017). Many small habitat patches seem to host more species than a few large patches of the same total area (Fahrig 2020). However, loss of habitat amount can negatively impact biodiversity, as it can limit the movement and gene flow of many species, increasing the risk of extinction and altering the species composition within habitat patches (Fahrig 2003; Tremlová and Münzbergová 2007). Conservation efforts may aim to restore habitat amount and connectivity between fragments to mitigate negative impacts (Wilson et al. 2016). Ensuring adequate habitat size and connectivity is crucial for maintaining biodiversity, promoting ecosystem health and supporting the resilience of species and ecosystems in the face of changing environmental conditions (Correa-Ayram et al. 2016).

Fragmentation can pave the way for non-native plant species to establish and spread, which may lead to adverse ecological impacts (Keller et al. 2008; Gutiérrez et al. 2014). Invasive plant species typically compete with native plants for resources like water, nutrients, light, and space or even pollinators, leading to reduced native vegetation diversity and a shift in the structure and composition of plant communities (Crooks 2002). These changes can have cascading effects on the whole ecosystem (Diez et al. 2010), including changes to the food web and the availability of animal nesting and foraging sites. For instance, invasive plants may not provide pollinators with the same quality or quantity of food resources as native plants (Bjerknes et al. 2007). This can lead to a reduction in pollinator densities, which can affect the reproductive success of native plants and the availability of fruits and seeds for their consumers.

Common milkweed (*Asclepias syriaca*) is native to North America. It is a herbaceous perennial plant that grows 30–180 cm tall and produces clusters of fragrant, pink or purple flowers in the summer. Common milkweed provides food and habitat for a wide variety of wildlife, including many specialists (Spaeth et al. 2022). Therefore, common milkweed has high nature conservation value in its native range; however, its invasiveness should be carefully monitored and managed outside of its native range (Zalai et al. 2017). In Europe, the common milkweed is considered an invasive species in several countries, and it is included in the list of invasive alien species of the European Union (EU list 2017). It was originally introduced to Europe in the 17th century as an ornamental plant and by beekeepers as a key food resource for honeybees due to its large quantities of nectar and pollen (Bukovinszky et al. 2014). Common milkweed was introduced to Hungary in the 18th century by beekeepers to increase food availability for their bees and improve the health and productivity of their hives. Milkweed became invasive and spread rapidly in the lowland areas of Central Europe (Bakacsy and Bagi 2020).

Milkweed has a negative effect on the native, habitat specialist plants. The most vulnerable areas to milkweed invasion are those where the sandy soils have been degraded, and habitat disturbance is already threatening the native vegetation of grasslands (e.g. disturbed by overgrazing, Bakacsy and Bagi 2020) and forest plantations (e.g. disturbed by intensive forestry, Ingle et al. 2019). Due to its aggressive growth habit, common milkweed can dominate and displace other plant species. Milkweed has a positive effect on habitat generalist and forest plants (Gallé et al. 2023).

Furthermore, it negatively affects grassland species, especially those with low competitive ability (Kelemen et al. 2016; Berki et al. 2023). Therefore, milkweed invasion has a general negative effect on the nature conservation value of invaded habitats. The presence of milkweed also alters vegetation structure, it increases the total cover and vegetation height and decreases bare ground cover (Gallé et al. 2023).

One of the most threatened habitat types by milkweed invasion is the forest steppes in southern Hungary (Bakacsy and Bagi 2020). Forest steppes are a mosaic of forest patches on grasslands (Fig. 1a). They form a distinct vegetation belt, a transition between closed forests and mostly treeless steppes in Eastern Europe and Asia (Bátori et al. 2018). Only small fragments of forest steppe remained in Southern Hungary, where fragment size and habitat connectivity are important drivers of arthropod diversity, especially in the forest-steppe grasslands (Gallé et al. 2022a), generally exerting a stronger effect on habitat specialist than generalist arthropods (Gallé et al. 2023).

Arthropods are essential parts of ecosystems, fulfilling multiple roles, such as herbivores, pollinators, predators, decomposers and prey for other organisms

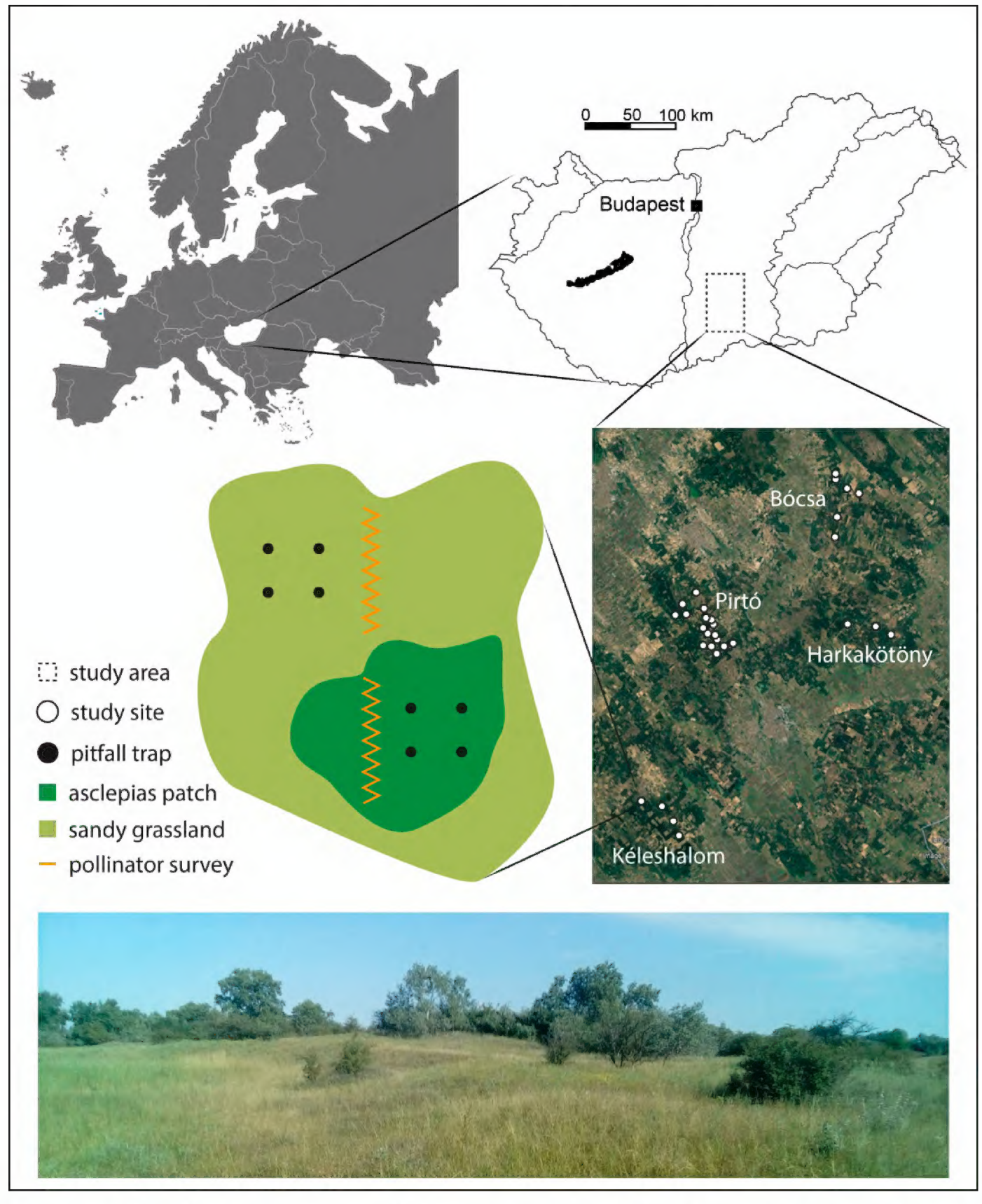

Figure 1. Map of study area showing the habitat fragments and the schematic figure of within-fragment sampling design.

(Schowalter 2022). Several factors affect arthropods' species and trait state composition. Focusing on functional traits can identify mechanisms that determine the impact of biodiversity on ecosystem processes (Spasojevic et al. 2018; Gallé and Batáry 2019). Identifying the drivers behind the trait state composition of arthropod communities can help us better understand their role in ecosystems and preserve their biodiversity (Haddad et al. 2008). The proliferation of an invasive plant, such as milkweed, may alter ecosystems, negatively impacting ground-dwelling arthropod populations (Gallé et al. 2015; Ingle et al. 2019). For example, Šeat et al. (2024) found that larger true bugs and species with generalist diets were associated with invasive plants in saline grasslands. Plant invasion may support web builders, reflecting vegetation composition and structural changes (Gomes et al. 2018). Connectivity and larger fragment size support large arthropod species, which can be expected to be good dispersers (Kormann et al. 2015, Korányi et al. 2023). Milkweed may affect wild bees positively, neutrally, and negatively (Szigeti et al. 2020; Kovács-Hostyánszki et al. 2022). The impact of common milkweed on wild bees depends on their traits, the local ecosystem and the abundance and distribution of other food and habitat resources (Gustafson et al. 2023).

In this study, we aimed to reveal the combined effects of milkweed invasion and habitat fragmentation on the functional diversity of three arthropod groups: herbivorous true bugs, wild bees and predatory spiders. We expected that (1) trait state and species composition differ between arthropod assemblages in invaded and non-invaded areas. We expected that varying connectivity and fragment size also shape trait composition: (2) Species dispersing over longer distances are able to populate less connected small fragments, whereas those with poor dispersal ability may be typical of well-connected large fragments; (3) Invasion homogenises food resources; thus species with a generalist diet are expected in invaded patches whereas feeding specialists are expected in areas that are close to natural.

Materials and methods

Study site and sampling design

We conducted our study in Southern Hungary (Fig. 1). This area is characterised by calcareous sandy alluvial soil with poor water retention capacity. The climate is continental, with 500–600 mm annual mean precipitation, and the mean annual temperature ranges from 10.2–10.8 °C (Török et al. 2003). The combined effect of climate and soil conditions allows the formation of forest-steppe vegetation community. Small patches of natural poplar forests (*Populus alba*), including juniper (*Juniperus communis*) and hawthorn bushes (*Crataegus monogyna*), are embedded in steppe grassland. The most common plant species of the steppe grasslands include *Festuca vaginata* and *Stipa borysthenica.* In the last century, vast natural forest steppes were converted into forest plantations of poplar and non-native pine trees and arable fields. The milkweed can spread easily in this region and form viable populations, especially in the grassland part of the remaining forest steppe fragments (Szitár et al. 2018).

We selected 30 forest-steppe fragments in a matrix of forest plantations along orthogonal gradients of fragment size and connectivity. Sampling sites were spatially clustered around four villages (Fig. 1). We conducted our samplings on the grasslands with similar vegetation characterised by dry bunchgrass steppes.

In each fragment, we established a pair of invaded vs. non-invaded (control) patches. Invaded patches had a milkweed stem density between 3–16/m^2. We selected invaded patches that covered at least 500 m^2, and sampling was done in the centre of the patch. Similarly, we sampled the centre of at least 500 m^2 non-invaded patches. Herbaceous vegetation was somewhat higher and denser in invaded patches than in non-invaded patches (Gallé et al. 2023). We avoided the edges of forest-steppe fragments, hence all sampling was done at least 40 m from the edges. We measured the size of the fragments using Quantum GIS 3.6.1 software and satellite images (Quantum GIS Development Team 2019). The size of the fragments varied between 0.2 and 8.7 ha and the distance to the nearest fragment varied between 15 m and 570 m. We also calculated the connectivity of fragments using Hanski's connectivity index within a buffer of 500 m around all fragments (Hanski et al. 2000), which seems to be appropriate in studying forest-steppe arthropods of the region (Gallé et al. 2022 a,b). Connectivity values ranged between 0 (isolated) and 705 (well-connected).

We used pitfall traps equipped with a funnel and a roof to collect ground-dwelling arthropods (Császár et al. 2018). We installed four traps at each sampling patch five meters from each other, in a square (Fig. 1). Traps were deployed for two weeks (9–27 July 2021) and we emptied the traps after one week. We identified true bugs and spiders at the species level. The data from the four traps was pooled for each patch.

We surveyed flower-visiting insects (wild bees belonging to the Hymenoptera order except for honeybees) using the transect method (50 m-long zig-zag transect surveyed for 15 minutes) (Fig. 1). We excluded honeybees as their presence was dependent on the presence of farmers' hives. We recorded all wild bees at a distance of 2.5 m to the right and left sides of the transect. Sampling was carried out by the same person (ET). All wild bees that could not be identified in the field were collected with standard entomological nets, stored in 70% ethanol and identified with a stereomicroscope. We performed two sampling rounds, the first at the beginning of the milkweed flowering period (10.06.-15.06.2021) and the second at the peak of the flowering period (28.06.-02.07.2021). Voucher specimens were placed in the arthropod collection of the HUN-REN Centre for Ecological Research (spiders and hymenopterans) and the University of Szeged (true bugs).

Arthropod functional traits

Body size of all species was given as a continuous variable in mm (mean body length averaged over males and females). For the other traits, we used ordinal categories. For true bugs, we used the wing length as a proxy for dispersal ability (0 – brachypterous, 0.25 – predominantly brachypterous, 0.5 – equally brachypterous and macropterous, 0.75 – predominantly macropterous, 1 – macropterous), and their diet range (0 – monophagous, 0.5 – oligophagous, 1 – polyphagous). For wild bees, social habit (0 – solitary, 0.5 – subsocial, 1 social) trait and nesting height (0 – in the soil, 0.5 – on herbaceous vegetation, 1 – tree trunk) was used. In the case of spiders, we took into account their dispersal ability, which was indicated by the ballooning trait (0 – the species is not likely to balloon, 0.5 – at least a single species is known to balloon in the genus, 1 – the species balloon) and their hunting strategy (0 – active ground hunters, 0.5 – ambush hunters on vegetation, 1 – web-builders).

In order to moderate the weight of the large values, trait values ranged between 0 and 1 (Suppl. material 1). Trait values were collected from the following literature: Panizzi and Grazia (2015), Wachmann et al. (2008), Bees, Wasps and Ants Recording Society (BWARS 2021), Witt (1998), Falk (2015), Cardoso et al. (2011), Bell et al. (2005), Blandenier (2009) and Nentwig et al. (2017).

Data analyses

We calculated the community-weighted means (CWM) for each trait, using the averages of trait values weighted by the relative abundances of each species at each sampling site. We applied linear mixed-effects models to investigate the effect of invasion, fragment size, connectivity and their two-way interactions on arthropod communities (lmer function in package lme4, Bates 2010). We log-transformed fragment size values before the analyses. We included the fragment ID nested in the nearest village (corresponding to the spatial clusters of fragments) in the model as a random effect to consider potential spatial autocorrelation. We used diagnostic figures (Q-Q plots, residuals vs. fitted values) to check whether the model assumptions were met. We transformed response variable data if we detected deviation from model assumptions (see Table 1, for details). Furthermore, we used Cook's distance (Cook 1979) to measure an observation's influence on the

Table 1. Summary table for linear mixed-effects model results on true bug, wild bee and spider communities showing model parameter estimates of each variable ± 95% confidence intervals. Significant p-values at $p < 0.05$ are indicated in bold. "Invasion" refers to the presence of invasive milkweed; we kept non-invaded as the reference factor level for "Invasion".

Herbivores	**Size**[1]	**Dispersal**	**Diet**[2]
Invasion	**-0.340 ± 0.257**	0.129 ± 0.156	**-0.435 ± 0.224**
Fragment size	-0.205 ± 0.534	0.112 ± 0.292	-0.102 ± 0.407
Connectivity	-0.334 ± 0.504	**0.291 ± 0.263**	0.099 ± 0.386
Invasion × Fragment size	-0.155 ± 0.361	0.005 ± 0.219	**0.479 ± 0.315**
Invasion × Connectivity	**0.425 ± 0.348**	-0.141 ± 0.210	**0.400 ± 0.304**
Fragment size × Connectivity	0.150 ± 0.935	-0.307 ± 0.474	-0.533 ± 0.700
Bees	**Size**[3]	**Nesting**[4]	**Social habit**
Invasion	0.041 ± 0.372	**-0.283 ± 0.262**	-0.017 ± 0.410
Fragment size	-0.311 ± 0.778	-0.241 ± 0.431	-0.101 ± 0.676
Connectivity	-0.037 ± 0.742	-0.242 ± 0.407	0.324 ± 0.639
Invasion × Fragment size	0.309 ± 0.522	**0.443 ± 0.368**	0.388 ± 0.577
Invasion × Connectivity	0.005 ± 0.504	0.252 ± 0.355	-0.131 ± 0.294
Fragment size × Connectivity	0.358 ± 1.379	0.367 ± 0.713	-0.133 ± 0.861
Predators	**Size**[5]	**Dispersal**	**Hunting**[4]
Invasion	-0.268 ± 0.264	-0.096 ± 0.132	0.060 ± 0.096
Fragment size	0.272 ± 0.469	-0.208 ± 0.274	0.073 ± 0.158
Connectivity	0.339 ± 0.431	**-0.320 ± 0.259**	-0.037 ± 0.149
Invasion × Fragment size	0.154 ± 0.388	-0.015 ± 0.186	-0.088 ± 0.135
Invasion × Connectivity	0.238 ± 0.375	**0.227 ± 0.181**	-0.020 ± 0.130
Fragment size × Connectivity	-0.796 ± 0.761	0.432 ± 0.509	0.083 ± 0.264

[1] variable was inverse transformed and ranged between 0 and 1.
[2] variable was qubic transformed and ranged between 0 and 1.
[3] variable was box-cox ($\lambda = 2.1$) transformed and ranged between 0 and 1.
[4] model was refitted with zero-inflated generalised linear model.
[5] variable was log-transformed and ranged between 0 and 1.

coefficients' estimation. We checked the data for influential points with Cook's distance and did not detect any. We employed PERMANOVA using Bray-Curtis distance measure to examine the multivariate response of arthropod communities to factors such as fragment size, connectivity, and the presence of milkweed (adonis2 function in vegan package Oksanen et al. 2019). If the PERMANOVA detected significant differences between arthropod communities of invaded and non-invaded habitat patches, we applied the indicator value analysis to identify characteristic species. We calculated the indicator value (IndVal) based on the relative frequency and average abundance of the species we sampled (Dufrêne and Legendre 1997, indval function in package labdsv, Roberts 2019). The statistical significances of the indicator values were estimated by 9999 random permutations of fragments across groups. We visualised the community composition of arthropods using non-metric multidimensional scaling (NMDS) with Bray-Curtis dissimilarity measure and 100 random starts with the vegan package (Oksanen et al. 2019). Prior to ordination, we transformed the species abundance data into relative species values by applying a Hellinger transformation. This transformation aimed to decrease the influence of species with high abundances (Legendre and Gallagher 2001). We used the R Studio software and the R statistical environment (R Core Team 2022) for all analyses.

Results

We collected 2797 true bug individuals belonging to 58 species, 854 wild bees belonging to 30 species and 2544 spiders representing 65 species (Suppl. material 1). The CWM of true-bugs body size increased with increasing connectivity in invaded patches but decreased in non-invaded ones. (Table 1, Fig. 2A). Connectivity had a significant positive effect on the wing length of true bugs, as there were more individuals with developed wings in well-connected fragments than in poorly connected fragments (Table 1, Fig. 2B). We found a similar pattern for fragment size and connectivity effect on herbivore diet as it was influenced by both fragment size and connectivity in interaction with invasion. The diet of herbivorous true bugs became more specialised (i.e., the community shifted from polyphagous toward monophagous individuals) in non-invaded patches and increased in invaded fragments with increasing connectivity and fragment size (Table 1, Fig. 2C, D).

Bee individuals with higher nesting locations were more common in non-invaded patches. We also detected an interaction effect of invasion and fragment size on the CWMs of wild bees' nesting strategy. We found more ground-nesting wild bees in non-invaded patches in small than large fragments (Table 1, Fig. 3E).

The ballooning propensity, the proxy for the dispersal ability of spiders decreased (i.e. the number of poorly dispersing individuals increased) in non-invaded patches as connectivity increased. In contrast, in patches invaded by milkweed, CWM of dispersal ability values increased with increasing connectivity (Table 1, Fig. 3F).

We found significant differences in the wild bee and predator community composition of the invaded and the non-invaded patches (Table 2). We detected a single indicator wild bee species, namely *Bombus terrestris*, in the invaded habitats (Fig. 3A). In the case of predators, we found one indicator species, the salticid *Pellenes nigrociliatus*, for the non-invaded and three gnaphosid species, *Haplodrassus bohemicus*, *Zelotes exigus*, *Zelotes segrex* for the invaded fragments (Fig. 3B). No differences in community composition were observed for herbivores (Table 2).

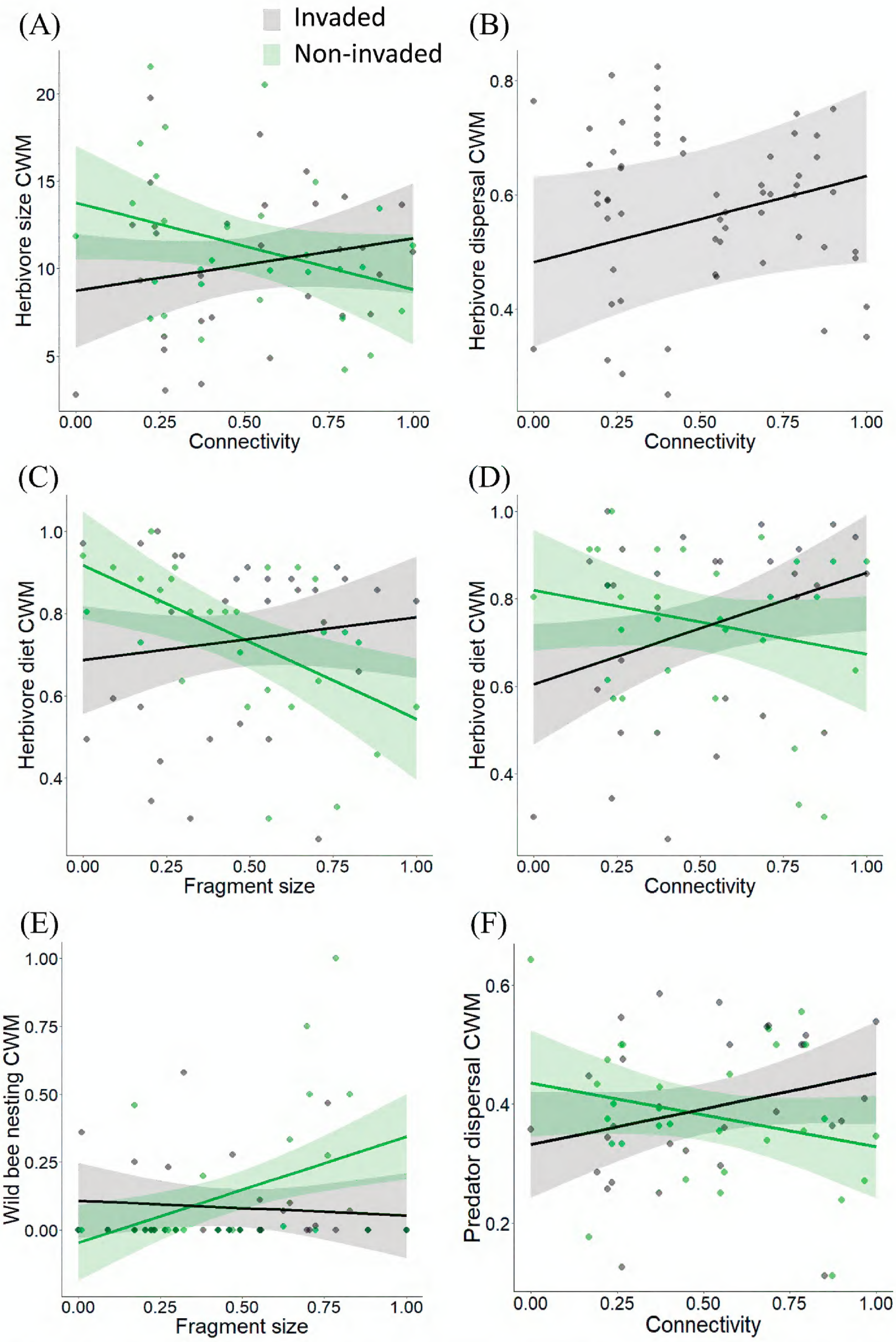

Figure 2. Effects of invasion and landscape variables on arthropod functional trait CWMs (community weighted mean). These are abundance-weighted averages of indices ranging from 0-1 (see Methods) **A** interacting effect of milkweed invasion and connectivity on herbivore size CWM **B** connectivity affect dispersal CWM of herbivores **C** invasion and fragment size effect on herbivore diet CWM **D** the interacting effect of invasion and on the diet CWMs of herbivores **E** interacting effect of invasion and fragment size on wild bee species nest height CWM **F** interacting effect of invasion and fragment size on spider dispersal CWM. Ranged values of connectivity and log-transformed fragment size are plotted. Grey dots show invaded sites and green dots show non-invaded sites. We show fitted regression lines with 95% confidence intervals.

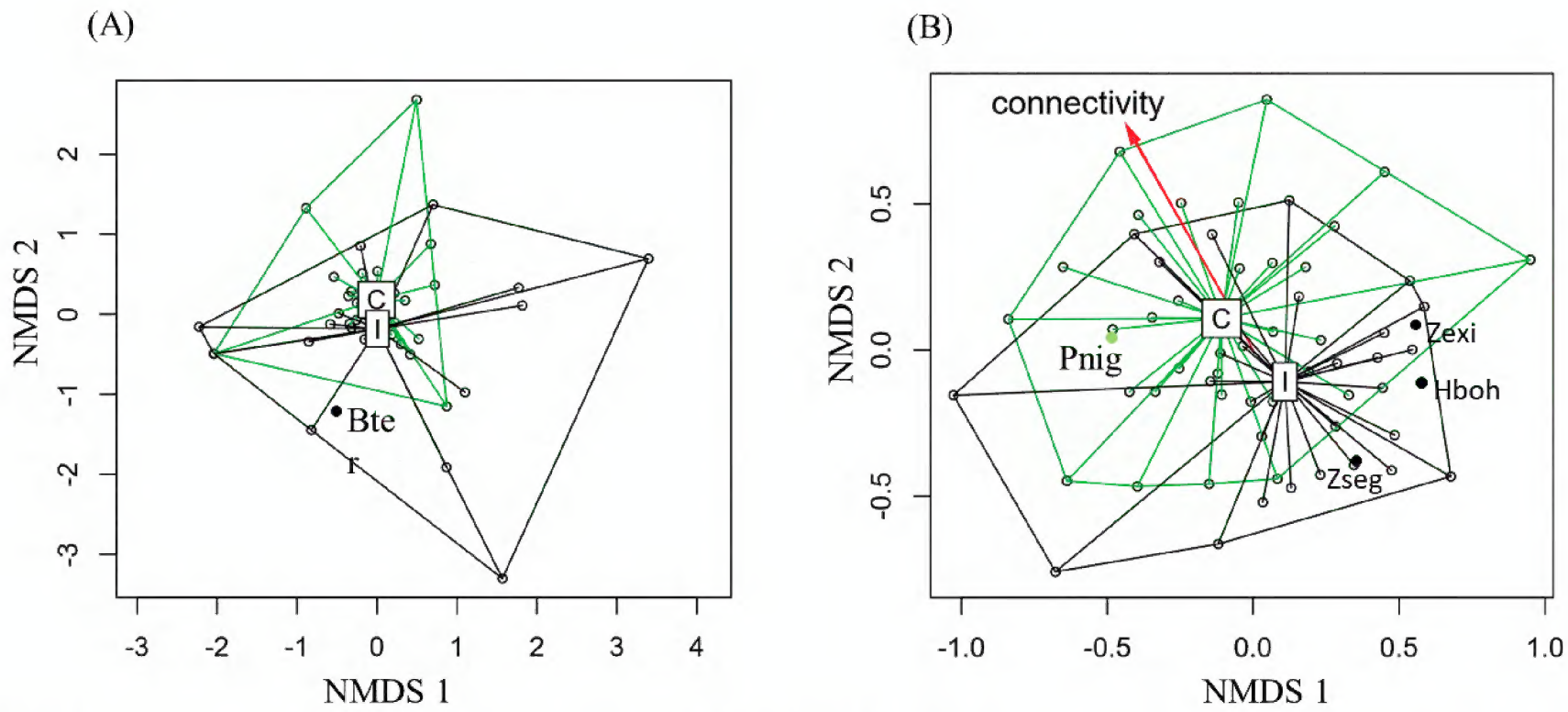

Figure 3. Non-metric multidimensional scaling ordination (NMDS) of **A** wild bee (stress = 0.073), and **B** predator (stress = 0.260) community composition. Sites are indicated with open circles. Red arrow indicates the significant continuous variable, and convex hulls indicate the habitat (C: control (non-invaded), I: invaded). Indicator species of invaded areas are indicated with black dots, and indicator species of non-invaded areas are green dots. Bter: *Bombus terrestris* (Apidae), Pnig: *Pellenes nigrociliatus* (Salticidae), Zexi: *Zelotes exigus* (Gnaphosidae), Hboh: *Haplodrassus bohemicus* (Gnaphosidae) and Zseg: *Zelotes segrex* (Gnaphosidae).

Table 2. PERMANOVA results for studied arthropod communities. Significant p-values are indicated in bold ($p < 0.05$).

	Herbivore			Wild bees			Predator		
	R^2	F	*P*	R^2	F	*p*	R^2	F	*p*
Invasion	0.030	1.788	0.083	0.035	2.097	**0.033**	0.034	2.108	**0.011**
Connectivity	0.016	0.970	0.456	0.009	0.548	0.861	0.032	1.973	**0.017**
Fragment size	0.004	0.293	0.978	0.020	1.217	0.256	0.019	1.196	0.260

Discussion

We studied the effect of invasive milkweed, fragment size, and connectivity on different arthropod communities inhabiting a threatened habitat type, the forest steppe. We found an interacting effect of the presence of the invasive species, connectivity and fragment size affected on most arthropod traits. Specifically, our hypothesis (1) was supported: invasion or its interaction with fragment size or connectivity affected the traits of all arthropods studied. Hypothesis (2) was also supported: the presence of the invasive plant shaped the community composition of wild bees and spiders. Hypothesis (3) was supported for true bugs in well-connected fragments: we found more polyphagous herbivores in invaded sites than in non-invaded sites.

Corridors or interconnected patches facilitate large individuals' movement, increasing the likelihood of their presence, but this effect was not attributed to a single or few species. Large herbivores typically require ample food resources to sustain their larger body size (Tscharntke et al. 2002). Herbivore body size increased with higher connectivity in non-invaded but decreased in invaded patches. This suggests that smaller herbivorous insects might be more common in well-connected habitats. But the presence of invasive plants filters for smaller species and disadvantaging the larger species in poorly connected habitats.The collected true bug species mainly rely on native plants, generally avoiding milkweed, as this plant is poisonous to many herbivores. Only a few European true bug species feed on

the milkweed, from the genus *Lygaeus*. Indeed, we collected more *Lygaeus simulans* individuals in invaded (34 individuals, 77%) than in non-invaded areas (10 individuals, 22%). Native plants of the forest-steppe grasslands can be more accessible and readily available in non-invaded patches, promoting the occurrence of larger true bug species. If the preferred host plants of a true bug species are negatively affected by invasive plants, this can lead to a decline in the abundance of that true bug species (Crooks 2002). This may occur despite increasing habitat connectivity.

In line with our expectations, large and well-connected fragments supported feeding specialists if fragments were non-invaded (e.g. Fischer and Lindenmayer 2007). The herbivore community shifted towards species with specialist diets in non-invaded patches, but in invaded patches, the generalist species were more frequent with increasing connectivity and fragment size. This suggests that invasive plants can affect herbivores' feeding specialisation, resulting in more generalists in large and connected fragments. The presence of invasive milkweed can have a negative impact on herbivores both directly and indirectly (Gallé et al. 2023; Korányi et al. 2023). Herbivores encounter invasive plants with chemical compositions that differ significantly from those of native plants (Xiao et al. 2020). Native herbivores are not adapted, or are poorly adapted, to feed on invasive plants. The indirect effect of milkweed on feeding specialisation might have been established through the effect of the invasive plant on native vegetation. Invasive plants negatively affect the native plant communities (Vilà et al. 2011). Consequently, they may reduce the access of specialist herbivores to their native host plants. Milkweed affects the species composition of native vegetation by supporting more generalist plant species, which provide a more diverse diet for generalist true bugs (Gallé et al. 2023). Moreover, milkweed can provide shade through its canopy and litter, potentially alleviating unfavourable abiotic (microclimate) conditions for the germination of specialist plant species (Szitár et al. 2018). Furthermore, the large stems of milkweed change the habitat structure of sandy grasslands, presumably reducing the availability of suitable oviposition sites and compromising herbivores' survival and reproductive success (Tallamy and Shropshire 2009). The generalist plants in invaded patches might formed a suitable habitat for generalist herbivores; therefore, connectivity and fragment size supported their high abundance.

The availability of suitable nesting sites is crucial for solitary wild bees, making them highly vulnerable to unfavourable environmental factors and the impacts of human-induced changes (Harmon-Threatt 2020). Milkweed was the highest herbaceous plant species in our study, producing large quantities of relatively high stems. Above-ground nesting bees build their nests in holes in plant stems or dead wood (Bihaly et al. 2021). The increased ratio of wild bees nesting on higher vegetation in non-invaded patches means that large milkweed stems did not offer more suitable nesting sites for above-ground nesters. Additionally, the large fragments support a larger population of vegetation-nesters, presumably by offering more nesting sites and more available food resources. Minimising the distance wild bees have to cover between the food resource and nesting location during foraging is essential to allocating energy for their reproduction. Non-invaded patches bear lower average vegetation heights and more bare soil surfaces, which create ideal conditions for ground-nesting species (Harmon-Threatt 2020). The majority of recorded bee species nest in the soil and spend much of their life cycle underground. Their preferences may differ concerning soil type, texture, compaction, moisture, and temperature (Antoine and Forrest 2021). Lower soil moisture and lower ground surface temperatures caused by milkweed invasion (Gallé et al. 2023) could poten-

tially limit ground-nesting species (Pellaton et al. 2024), however ground-nesting bees generally dominated the communities of forest-steppe fragments. Large and well-connected, flower-rich forest-steppe fragments are beneficial for ground-nesting bees (Török et al. 2022). Further, the impact of milkweed invasion on different floral visitor groups may vary, as their diversity is probably influenced by the presence and variety of native flowering resources (Kovács-Hostyánszki et al. 2022). However, it did not affect the size and social behaviour of wild bees.

Well-connected fragments are often viewed as higher-quality habitats with more specialist species. They support a high species richness and abundance of arthropods (Hanski 1998), which are potential food items for predators, provide suitable conditions and high-quality habitats for many spiders including poorly dispersing species (Gallé et al. 2022a). In sandy grasslands, vegetation structure is also among the most important parameters that affects spiders (Carvalho et al. 2011). Specifically, vegetation with complex structures supports many spider species (Gallé et al. 2010). Milkweed increases vegetation complexity, and, therefore might have an indirect positive effect on spiders and change trait state composition of the community. We found that predator dispersal ability decreased with connectivity in non-invaded patches, but increased in patches invaded by milkweed.

Spiders with good dispersal ability can move between fragments more efficiently in landscapes with well-connected fragments, facilitating gene flow and maintaining stable populations (Gallé et al. 2022b). In contrast, limited connectivity hinders the movement of spiders with poor dispersal ability, as they may not be able to traverse the vast distances between patches effectively (Gallé et al. 2022c). Consequently, these spiders are more likely to remain confined within their habitat patch and have limited opportunities to disperse or colonise new areas.

The differences in community composition between invaded and non-invaded patches of wild bees and predators could be because invasive species can alter the availability and quality of resources (Bartomeus et al. 2008) and habitats for these groups (Pyšek and Richardson 2007), leading to changes in their community composition. Indicator species were the most sensitive to the differences in the conditions between invaded and non-invaded habitats. We found a single indicator wild bee species for invaded patches, *B. terrestris*, an abundant ground-nesting bumblebee species in Europe. Our results showed that milkweed flowers attract *B. terrestris*. This highly mobile insect can fly over 1 km for flower resources (Osborne et al. 2008). Due to its high foraging range and sufficient tongue length to access the nectar of milkweed flowers, it is one of the few polylectic bee species that can utilise the milkweed nectar (Kephart and Theiss 2004). In invaded patches, the large quantity of nectar provided by milkweed might distract pollinating insects that are capable of utilising milkweed nectar away from native plants and affecting their pollination services of native plants (Goulson et al. 2010), with a potential negative long-term impact on them (Kovács-Hostyánszki et al. 2022).

In invaded habitats, alterations in the availability of potential spider prey associated with milkweed invasions may have cascading effects on spider populations. In our study, we found significant differences in predator community composition between invaded and non-invaded patches, with a single indicator species (*P. nigrociliatus*) preferring non-invaded vegetation and avoiding invaded patches. Three indicator species of invaded patches (*H. bohemicus*, *Z. exigus*, *Z. segrex*) were xerophilous species. The presence of milkweed provides drier and more favourable conditions for these species (Gallé et al. 2023).

Our study highlights the complex interactions between fragmentation and invasion on ecological traits of herbivores, wild bees, and predators. Our research revealed that fragmentation and invasions interacted, typically altering their respective impacts by selectively favouring opposite trait levels. Our results suggest that invasive species can significantly impact the traits of arthropods and that larger and better-connected fragments may not necessarily provide better habitats. Therefore, we suggest that restoration projects should aim to restore habitats and their connectivity and eliminate invasive species from natural habitats. This may involve targeted removal or control of invasive species while promoting the recovery of native species and their ecological interactions. Future research should focus on the effects of milkweed removal on plants and arthropods, including detailed food web analyses, assessing the direct and indirect effects of management (e.g. via altered habitat parameters) and providing an opportunity to identify species that are sensitive to or supported by management interventions. Given the complexity of interactions between fragmentation (size and connectivity) and invasion, adaptive management approaches incorporating ongoing monitoring and evaluation are crucial.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Funding

This research received support from the Hungarian National Research, Development and Innovation Office (within the framework of National Laboratory for Health Security RRF 2.3.1-21-2021-00006 and NKFIH KKP 133839, NKFIH-FK-142926).

Author contributions

RG, PB: Conceptualization, RG: Methodology, Software, Validation, Formal analysis, RG, ARS, ET, LT, DK, AT, G-SN: Investigation, RG, PB: Resources, Funding Acquisition, RG, G-SN: Data Curation, RG, ARS: Writing – Original draft, RG, ARS, ET, LT, DK, AT, G-SN, PB: Writing – Review and Editing, G-SN: Visualization.

Author ORCIDs

Róbert Gallé https://orcid.org/0000-0002-5516-8623
Edina Török https://orcid.org/0000-0001-5982-7078
Tamás Lakatos https://orcid.org/0000-0002-4414-8459
Dávid Korányi https://orcid.org/0000-0002-0101-0425
Attila Torma https://orcid.org/0000-0002-9412-2265
Nikolett Gallé-Szpisjak https://orcid.org/0000-0001-7871-3834
Péter Batáry https://orcid.org/0000-0002-1017-6996

Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

References

Antoine CM, Forrest JRK (2021) Nesting habitat of ground-nesting bees: A review. Ecological Entomology 46(2): 143–159. https://doi.org/10.1111/een.12986

Bakacsy L, Bagi I (2020) Survival and regeneration ability of clonal common milkweed (*Asclepias syriaca* L.) after a single herbicide treatment in natural open sand grasslands. Scientific Reports 10(1): 14222. https://doi.org/10.1038/s41598-020-71202-8

Bartomeus I, Vilà M, Santamaría L (2008) Contrasting effects of invasive plants in plant–pollinator networks. Oecologia 155(4): 761–770. https://doi.org/10.1007/s00442-007-0946-1

Bates DM (2010) lme4: Mixed-effects modeling with R.

Bátori Z, Erdős L, Kelemen A, Deák B, Valkó O, Gallé R, Bragina TM, Kiss PJ, Kröel-Dulay G, Tölgyesi C (2018) Diversity patterns in sandy forest-steppes: A comparative study from the western and central Palaearctic. Biodiversity and Conservation 27(4): 1011–1030. https://doi.org/10.1007/s10531-017-1477-7

BWARS (2021) Bees, Wasps and Ants Recording Society. http://www.bwars.com/ [Accessed 08 February 2021]

Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk: World fauna, phylogenies, genetics and models. Bulletin of Entomological Research 95(2): 69–114. https://doi.org/10.1079/BER2004350

Berki B, Botta-Dukát Z, Csákvári E, Gyalus A, Halassy M, Mártonffy A, Rédei T, Csecserits A (2023) Short-term effects of the control of the invasive plant Asclepias syriaca: Secondary invasion of other neophytes instead of recovery of the native species. Applied Vegetation Science 26(1): e12707. https://doi.org/10.1111/avsc.12707

Bihaly ÁD, Kovács-Hostyánszki A, Szalai M, Sárospataki M (2021) Nesting activity of cavity-nesting bees and wasps is lower in small-scale apple orchards compared to nearby semi-natural habitats. Agricultural and Forest Entomology 23(1): 49–58. https://doi.org/10.1111/afe.12403

Bjerknes AL, Totland Ø, Hegland SJ, Nielsen A (2007) Do alien plant invasions really affect pollination success in native plant species? Biological Conservation 138(1–2): 1–12. https://doi.org/10.1016/j.biocon.2007.04.015

Blandenier G (2009) Ballooning of spiders (Araneae) in Switzerland: general results from an eleven-year survey. Arachnology 14: 308–316. https://doi.org/10.13156/arac.2009.14.7.308

Bukovinszky T, Gols R, Agrawal AA, Roge C, Bezemer TM, Biere A, Harvey JA (2014) Reciprocal interactions between native and introduced populations of common milkweed, Asclepias syriaca, and the specialist aphid, Aphis nerii. Basic and Applied Ecology 15(5): 444–452. https://doi.org/10.1016/j.baae.2014.07.004

Cardoso P, Pekár S, Jocqué R, Coddington JA (2011) Global patterns of guild composition and functional diversity of spiders. PLoS ONE 6(6): e21710. https://doi.org/10.1371/journal.pone.0021710

Carvalho JC, Cardoso P, Crespo LC, Henriques S, Carvalho R, Gomes P (2011) Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. Diversity & Distributions 17(2): 225–234. https://doi.org/10.1111/j.1472-4642.2010.00731.x

Cook RD (1979) Influential observations in linear regression. Journal of the American Statistical Association 74(365): 169–174. https://doi.org/10.1080/01621459.1979.10481634

Correa-Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: A review of recent studies and applications. Progress in Physical Geography 40(1): 7–37. https://doi.org/10.1177/0309133315598713

Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. Oikos 97(2): 153–166. https://doi.org/10.1034/j.1600-0706.2002.970201.x

Császár P, Torma A, Gallé-Szpisjak N, Tölgyesi C, Gallé R (2018) Efficiency of pitfall traps with funnels and/or roofs in capturing ground-dwelling arthropods. European Journal of Entomology 115: 15–24. https://doi.org/10.14411/eje.2018.003

Diez JM, Dickie I, Edwards G, Hulme PE, Sullivan JJ, Duncan RP (2010) Negative soil feedbacks accumulate over time for non-native plant species. Ecology Letters 13(7): 803–809. https://doi.org/10.1111/j.1461-0248.2010.01474.x

Dufrêne M, Legendre P (1997) Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs 67(3): 345–366. https://doi.org/10.2307/2963459

EU list (2017) Consolidated list of invasive alien species of Union concern. https://ec.europa.eu/environment/nature/invasivealien/list/index_en.htm

Fahrig L (2003) Effects of habitat fragmentation on biodiversity. Annual review of ecology, evolution, and systematics 34(1): 487–515. https://doi.org/10.1146/annurev.ecolsys.34.011802.132419

Fahrig L (2017) Ecological responses to habitat fragmentation per se. Annual Review of Ecology, Evolution, and Systematics 48(1): 1–23. https://doi.org/10.1146/annurev-ecolsys-110316-022612

Fahrig L (2020) Why do several small patches hold more species than few large patches? Global Ecology and Biogeography 29(4): 615–628. https://doi.org/10.1111/geb.13059

Falk S (2015) Field Guide to the Bees of Great Britain and Ireland. Bloomsbury Publishing.

Fischer J, Lindenmayer DB (2007) Landscape modification and habitat fragmentation: A synthesis. Global Ecology and Biogeography 16(3): 265–280. https://doi.org/10.1111/j.1466-8238.2007.00287.x

Gallé R, Batáry P (2019) Trait-based paradise – About the importance of real functionality. Community Ecology 20(3): 314–316. https://doi.org/10.1556/168.2019.20.3.11

Gallé R, Torma A, Körmöczi L (2010) Small-scale effect of habitat heterogeneity on invertebrate assemblages in sandy grasslands (Hungarian Great Plain). Polish Journal of Ecology 58: 333–346. https://doi.org/10.1007/s10980-018-0677-1

Gallé R, Erdélyi N, Szpisjak N, Tölgyesi C, Maák I (2015) The effect of the invasive Asclepias syriaca on the ground-dwelling arthropod fauna. Biologia 70(1): 104–111. https://doi.org/10.1515/biolog-2015-0011

Gallé R, Korányi D, Tölgyesi C, Lakatos T, Marcolin F, Török E, Révész K, Szabó ÁR, Torma A, Gallé-Szpisjak N, Marja R, Szitár K, Deák B, Batáry P (2022a) Landscape-scale connectivity and fragment size determine species composition of grassland fragments. Basic and Applied Ecology 65: 39–49. https://doi.org/10.1016/j.baae.2022.10.001

Gallé R, Tölgyesi C, Császár P, Bátori Z, Gallé-Szpisjak N, Kaur H, Maák I, Torma A, Batáry P (2022b) Landscape structure is a major driver of plant and arthropod diversity in natural European forest fragments. Ecosphere 13(1): e3905. https://doi.org/10.1002/ecs2.3905

Gallé R, Tölgyesi C, Torma A, Bátori Z, Lörinczi G, Szilassi P, Gallé-Szpisjak N, Kaur H, Makra T, Módra G, Batáry P (2022c) Matrix quality and habitat type drive the diversity pattern of forest steppe fragments. Perspectives in Ecology and Conservation 20(1): 60–68. https://doi.org/10.1016/j.pecon.2021.11.004

Gallé R, Tölgyesi C, Szabó ÁR, Korányi D, Bátori Z, Hábenczyus A, Török E, Révész K, Torma A, Gallé-Szpisjak N, Lakatos T, Batáry P (2023) Plant invasion and fragmentation indirectly and contrastingly affect native plants and grassland arthropods. The Science of the Total Environment 903: 166199. https://doi.org/10.1016/j.scitotenv.2023.166199

Gomes M, Carvalho JC, Gomes P (2018) Invasive plants induce the taxonomic and functional replacement of dune spiders. Biological Invasions 20(2): 533–545. https://doi.org/10.1007/s10530-017-1555-5

Goulson D, Lepais O, O' Connor S, Osborne JL, Sanderson RA, Cussans J, Goffe L, Darvill B (2010) Effects of land use at a landscape scale on bumblebee nest density and survival. Journal of Applied Ecology 47(6): 1207–1215. https://doi.org/10.1111/j.1365-2664.2010.01872.x

Gustafson NW, Couture JJ, Dalgleish HJ (2023) Herbivory, plant traits and nectar chemistry interact to affect the community of isect visitors and pollination in common milkweed, Asclepias syriaca. Oecologia 201(1): 91–105. https://doi.org/10.1007/s00442-022-05290-w

Gutiérrez JL, Jones CG, Sousa R (2014) Toward an integrated ecosystem perspective of invasive species impacts. Acta Oecologica 54: 131–138. https://doi.org/10.1016/j.actao.2013.10.003

Haddad NM, Holyoak M, Mata TM, Davies KF, Melbourne BA, Preston K (2008) Species' traits predict the effects of disturbance and productivity on diversity. Ecology Letters 11(4): 348–356. https://doi.org/10.1111/j.1461-0248.2007.01149.x

Hanski I (1998) Metapopulation dynamics. Nature 396(6706): 41–49. https://doi.org/10.1038/23876

Hanski I, Alho J, Moilanen A (2000) Estimating the parameters of survival and migration of individuals in metapopulations. Ecology 81(1): 239–251. https://doi.org/10.1890/0012-9658(2000)081[0239:ETPOSA]2.0.CO;2

Harmon-Threatt A (2020) Annual Review of Entomology Influence of Nesting Characteristics on Health of Wild Bee Communities. Annual Review of Entomology 65(1): 39–56. https://doi.org/10.1146/annurev-ento-011019-024955

Ingle K, Gallé-Szpisjak N, Kaur H, Gallé R (2019) Forest type interacts with milkweed invasion to affect spider communities. Insect Conservation and Diversity 12(4): 321–328. https://doi.org/10.1111/icad.12346

Kelemen A, Valkó O, Kröel-Dulay G, Deák B, Török P, Tóth K, Tóthmérész B (2016) The invasion of common milkweed (Asclepias syriaca) in sandy old-fields – is it a threat to the native flora? Applied Vegetation Science 19: 218–224. https://doi.org/10.1111/avsc.12225

Keller RP, Frang K, Lodge DM (2008) Preventing the spread of invasive species: Economic benefits of intervention guided by ecological predictions. Conservation Biology 22(1): 80–88. https://doi.org/10.1111/j.1523-1739.2007.00811.x

Kephart S, Theiss K (2004) Pollinator-mediated isolation in sympatric milkweeds (Asclepias): Do floral morphology and insect behavior influence species boundaries? The New Phytologist 161(1): 265–277. https://doi.org/10.1046/j.1469-8137.2003.00956.x

Korányi D, Gallé R, Torma A, Gallé-Szpisjak N, Batáry P (2023) Small grassland fragments and connectivity support high arthropod functional diversity in highly modified landscapes. Insect Conservation and Diversity 16(5): 701–711. https://doi.org/10.1111/icad.12668

Kormann U, Rösch V, Batáry P, Tscharntke T, Orci KM, Samu F, Scherber C (2015) Local and landscape management drive trait-mediated biodiversity of nine taxa on small grassland fragments. Diversity & Distributions 21(10): 1204–1217. https://doi.org/10.1111/ddi.12324

Kovács-Hostyánszki A, Szigeti V, Miholcsa Z, Sándor D, Soltész Z, Török E, Fenesi A (2022) Threats and benefits of invasive alien plant species on pollinators. Basic and Applied Ecology 64: 89–102. https://doi.org/10.1016/j.baae.2022.07.003

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129(2): 271–280. https://doi.org/10.1007/s004420100716

Nentwig W, Blick T, Gloor D, Hänggi A, Kropf C (2017) Spiders of europe. www.araneae.unibe.ch

Oksanen J, Blanchet F, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin P, O'Hara R, Simpson G, Solymos P (2019) vegan: Community ecology package. R package version 2.5-6.

Osborne JL, Martin AP, Carreck NL, Swain JL, Knight ME, Goulson D, Hale RJ, Sanderson RA (2008) Bumblebee flight distances in relation to the forage landscape. Journal of Animal Ecology 77(2): 406–415. https://doi.org/10.1111/j.1365-2656.2007.01333.x

Panizzi AR, Grazia J (Eds) (2015) True bugs (Heteroptera) of the Neotropics (Vol. 2). Springer, https://doi.org/10.1007/978-94-017-9861-7

Pellaton R, Szigeti V, Fenesi A, Roberts S, Török E, Kovács-Hostyánszki A (2024) The effects of plant invasion, floral resources and soil characteristics on ground-nesting bees. Journal of Insect Conservation 28(4): 843–854. https://doi.org/10.1007/s10841-024-00606-y

Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: where do we stand? Biological invasions. Springer, Berlin, Heidelberg, 97–125. https://doi.org/10.1007/978-3-540-36920-2_7

Quantum GIS Development Team (2019) Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Roberts DW (2019) labdsv: Ordination and Multivariate Analysis for Ecology. R package version 2.0-1.

Schowalter TD (2022) Insect ecology: an ecosystem approach. Academic press.

Šeat J, Torma A, Bátori Z, Popović M, Tölgyesi C (2024) Landscape matrix and substrate jointly shape the trait composition of true bug (Heteroptera) communities in drainage ditches. Biodiversity and Conservation 33(8–9): 1–18. https://doi.org/10.1007/s10531-024-02860-7

Spaeth Jr KE, Barbour PJ, Moranz R, Dinsmore SJ, Williams CJ (2022) Asclepias dynamics on US rangelands: Implications for conservation of monarch butterflies and other insects. Ecosphere 13(1): e03816. https://doi.org/10.1002/ecs2.3816

Spasojevic MJ, Catano CP, LaManna JA, Myers JA (2018) Integrating species traits into species pools. Ecology 99(6): 1265–1276. https://doi.org/10.1002/ecy.2220

Szigeti V, Fenesi A, Soltész Z, Berki B, Kovács-Hostyánszki A (2020) Neutral effect of an invasive plant species with specialized flower structure on native pollinator communities. Biological Invasions 22(10): 3017–3030. https://doi.org/10.1007/s10530-020-02305-6

Szitár K, Kröel-Dulay G, Török K (2018) Invasive Asclepias syriaca can have facilitative effects on native grass establishment in a water-stressed ecosystem. Applied Vegetation Science 21(4): 607–614. https://doi.org/10.1111/avsc.12397

Tallamy DW, Shropshire KJ (2009) Ranking lepidopteran use of native versus introduced plants. Conservation Biology 23(4): 941–947. https://doi.org/10.1111/j.1523-1739.2009.01202.x

Török K, Botta-Dukát Z, Dancza I, Németh I, Kiss J, Mihály B, Magyar D (2003) Invasion gateways and corridors in the Carpathian basin: Biological invasions in Hungary. Biological Invasions 5(4): 349–356. https://doi.org/10.1023/B:BINV.0000005570.19429.73

Török E, Gallé R, Batáry P (2022) Fragmentation of forest-steppe predicts functional community composition of wild bee and wasp communities. Global Ecology and Conservation 33: e01988. https://doi.org/10.1016/j.gecco.2021.e01988

Tremlová K, Münzbergová Z (2007) Importance of species traits for species distribution in fragmented landscapes. Ecology 88(4): 965–977. https://doi.org/10.1890/06-0924

Tscharntke T, Steffan-Dewenter I, Kruess A, Thies C (2002) Characteristics of insect populations on habitat fragments: A mini review. Ecological Research 17(2): 229–239. https://doi.org/10.1046/j.1440-1703.2002.00482.x

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P (2011) Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. Ecology Letters 14(7): 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Wachmann E, Melber A, Deckert J (2008) Wanzen 1–4. Die Tierwelt Deutschlands 75. Teil. Goecke & Evers.

Wilson MC, Chen XY, Corlett RT, Didham RK, Ding P, Holt RD, Holyoak M, Hu G, Hughes AC, Jiang L, Laurance WF, Liu J, Pimm SL, Robinson SK, Russo SE, Si X, Wilcove DS, Wu J, Yu M (2016) Habitat fragmentation and biodiversity conservation: Key findings and future challenges. Landscape Ecology 31(2): 219–227. https://doi.org/10.1007/s10980-015-0312-3

Witt R (1998) Wespen: beobachten, bestimmen, Naturbuch-Verlag, Augsbrug.

Xiao L, Ding J, Zhang J, Huang W, Siemann E (2020) Chemical responses of an invasive plant to herbivory and abiotic environments reveal a novel invasion mechanism. The Science of the Total Environment 741: 140452. https://doi.org/10.1016/j.scitotenv.2020.140452

Zalai M, Poczok L, Dorner Z, Körösi K, Pálinkás Z, Szalai M, Pintér O (2017) Developing control strategies against common milkweed (Asclepias syriaca L.) on ruderal habitats. Herbologia 16(2): 69. https://doi.org/10.5644/Herb.16.2.07

Supplementary material 1

List of species and trait values

Authors: Róbert Gallé, Ágota Réka Szabó, Edina Török, Tamás Lakatos, Dávid Korányi, Attila Torma, Nikolett Gallé-Szpisjak, Péter Batáry

Data type: docx

Explanation note: The trait values of species are given. For true bugs, we used the wing length as a proxy for dispersal ability (0 – brachypterous, 0.25 – predominantly brachypterous, 0.5 – equally brachypterous and macropterous, 0.75 – predominantly macropterous, 1 – macropterous), and their diet range (0 – monophagous, 0.5 – oligophagous, 1 – polyphagous). For wild bees, social habit (0 – solitary, 0.5 – subsocial, 1 social) trait and nesting height (0 – in the soil, 0.5 – on vegetation, 1 – tree trunk) was used. In the case of spiders, we took into account their dispersal ability, which was indicated by the ballooning trait (0 – the species is not likely to balloon, 0.5 – at least a single species is known to balloon in the genus, 1 – the species balloon) and their hunting strategy (0 – active hunters, 1 – web-builders).

Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.

Link: https://doi.org/10.3897/neobiota.98.139097.suppl1